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DYSMORODREPANIS MUNROI (FRINGILLIDAE: DREPANIDINI), A VALID GENUS AND SPECIES OF HAWAIIAN FINCH

HELEN F. JAMES, RICHARD L. ZUSI, AND STORRS L. OLSON[1]

ABSTRACT.—A Hawaiian finch that became extinct on the island of Lanai sometime after 1913 has been overlooked by ornithologists. Only one skin specimen of this bird was ever procured, and although it was described as the holotype of *Dysmorodrepanis munroi* Perkins, it soon fell into obscurity and was written off as a deformed example of *Psittirostra psittacea.* Our re-preparation and examination of the holotype indicates it is a valid genus and species. *Dysmorodrepanis* is probably most closely related to *Psittirostra psittacea,* and is distinguished by its unusual bill and associated modifications of the jaw apparatus, as well as by the plumage and external dimensions of the holotype. We speculate that the diastema between the bird's tomia may have allowed the bill tips to act as pincers. *Received 8 Oct. 1987, accepted 7 July 1988.*

Considerably after R. C. L. Perkins completed his major contributions to the natural history of the Hawaiian Islands, he introduced a new genus and species of bird, *Dysmorodrepanis munroi* (Perkins 1919), based on a single specimen collected by G. C. Munro on the island of Lanai in 1913. This is the only Hawaiian bird that Perkins formally named as new, despite his having made one of the most scholarly and original contributions to Hawaiian ornithology (Perkins 1903). Because the period following the description of *Dysmorodrepanis* was a quiescent one in Hawaiian ornithology, Perkins' new species was scarcely mentioned until Greenway (1939) examined the unique holotype and suggested that it was merely

[1] Dept. Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

an "aberrant young female" of the Ou, *Psittirostra psittacea.* Amadon (1950) concurred with Greenway, listing the species in the synonymy of *P. psittacea.* Until now there has been no further critical evaluation of this species, which had since been forgotten and ignored.

We initially were skeptical about the assignment of *Dysmorodrepanis munroi* to *P. psittacea* because of the external differences in bill form, plumage, and the smaller tarsus. We consequently had the holotype reprepared following the procedure described by Olson et al. (1987), in which the skull is removed and replaced in the skin with a cast. This allowed us to examine the cranial osteology and, to a limited extent, the myology of the specimen. We found no osteological evidence of a pathological condition that might have caused deformation of the bill in *Dysmorodrepanis*: rather, the cranium and mandible show morphological modifications concordant with the unusual bill form. We conclude that *Dysmorodrepanis munroi* is a valid genus and species of uniquely specialized drepanidine. Pending a more detailed character analysis of the Drepanidini, we consider *Dysmorodrepanis* to be a sister taxon of *P. psittacea,* and we tentatively cite the similar shape of the maxillary rostrum as a synapomorphous character linking these species. (Following Baumel et al. [1979], we refer to the external "mandibles" of the bill as the maxillary and mandibular rostra, and to the bony elements underlying these structures as the maxilla and mandible.)

Genus *Dysmorodrepanis* Perkins 1919:250

TYPE SPECIES.—*Dysmorodrepanis munroi* Perkins 1919, by monotypy.

DIAGNOSIS.—A medium-sized drepanidine finch in which the decurved maxillary rostrum overhangs the mandibular rostrum. Compared to other drepanidines with this condition, the maxillary rostrum is sturdy and finch-like, similar to *Pseudonestor xanthophrys* and *P. psittacea* (frontispiece, Fig. 1); it is not weak and attenuated like that of *Hemignathus* spp. (*sensu* Amadon 1950). The mandibular rostrum is strongly recurved, so that only its tip enters the ventral trough of the maxillary rostrum, leaving a conspicuous diastema between the tomia when the bill is closed (Fig. 2). The maxillary and mandibular rostra have deeply excavated internal surfaces. The tomial crests of both jaws from about the rostral third of the diastema to their tips are sharp and ridged as in *P. psittacea*; in the caudal two-thirds they curl inward to form broad, blunt surfaces that lie roughly parallel to each other at opposite sides of the diastema (Fig. 2). The articular cotylae and medial process of the mandible are rotated strongly caudad compared to their orientation in most birds. The ramus (pars intermedia) is shorter than in *P. psittacea* (Figs. 1 and 3). The quadrate-squamosal articulation is located more rostrally on the skull, and in the resting position the quadrate is rotated farther rostrad compared to *P. psittacea* or *Pseudonestor xanthophrys* (Figs. 1 and 4). The medial condyle of the quadrate is more elongate than in *P. psittacea,* but much less elongate than in *Pseudonestor* (Fig. 4). The palatines are similar to those in *P. psittacea* but shorter (Fig. 4). Perkins (1919) described the tongue as nontubular.

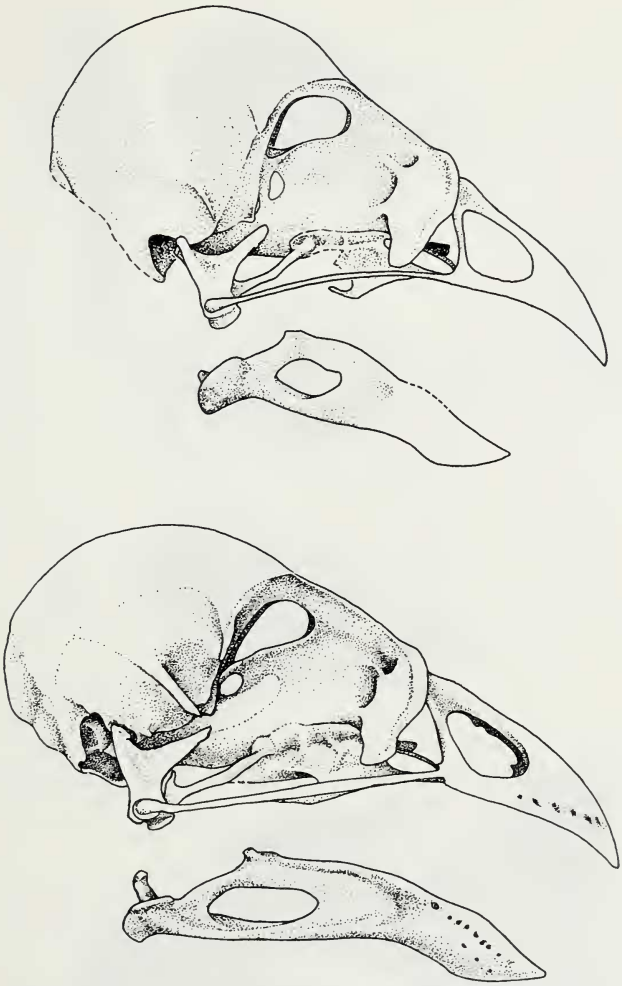

FIG. 1. Lateral view of the crania and mandibles of *Dysmorodrepanis munroi* (above) and *Psittirostra psittacea* (below).

DYSMORODREPANIS MUNROI PERKINS

Dysmorodrepanis munroi Perkins 1919:251.—Richmond 1927:12; Mathews 1930:814; Greenway 1939:479; Bryan and Greenway 1944:140; Greenway 1958:9; Munro 1944: 122; Munro 1960:191.

Desmodrepanis munroii.—Delacour 1928:22 (lapsus).

Psittirostra psittacea.—Amadon 1950:171; Greenway, 1968:101; Carlquist 1970:196.

Dysmodrepanis munroi.—Carlquist 1970:196 (lapsus, in synonymy).

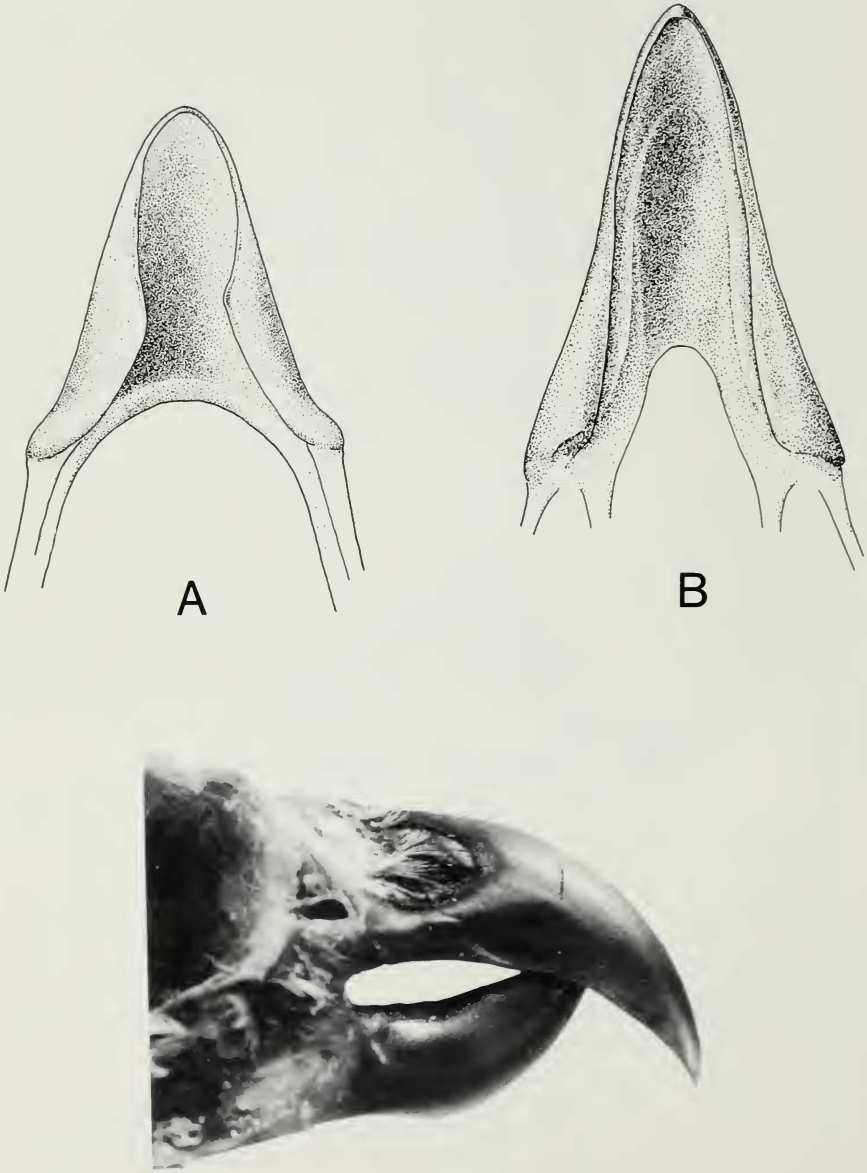

FIG. 2. The bill of *Dysmorodrepanis*. A) Dorsal aspect of the mandibular rostrum, B) ventral aspect of the maxillary rostrum, and C) photograph showing the relation of the rostra in closed position.

FIG. 3. X-radiograph of skins of (top) *Pseudonestor xanthophrys* USNM 177972, (middle) *Dysmorodrepanis munroi,* and (bottom) *Psittirostra psittacea,* USNM 169466.

HOLOTYPE.—Bernice P. Bishop Museum number BBM-4792, an unsexed skin of an adult bird collected and prepared by G. C. Munro on 22 February 1913. The fresh specimen measured six inches (152 mm) in length. J. P. Angle and F. V. Grady removed the skull and replaced it in the skin with an epoxy resin cast, December 1986, at the National Museum of Natural History, Smithsonian Institution. To preserve the unique morphology of the bill, the rhamphothecae were not removed from the two jaws. Archival-quality photographs and X-radiographs of the skin, taken before the skull was removed, are preserved in the photographic archives of the Bernice P. Bishop Museum, Honolulu, and at the Smithsonian Institution, Washington.

TYPE LOCALITY.—Kaiholena Valley, Island of Lanai, ca 20.83°N, 156.90°W, ca 2000 feet elevation.

DIAGNOSIS.—A drab Hawaiian finch with greenish olive plumage above and whitish yellow plumage below, with a yellowish superciliary stripe and whitish tips and inner vanes on the secondaries (frontispiece). The bird is the size of small females of *P. psittacea,* but the tarsometatarsus is proportionately short (Fig. 5). The non-overlapping dorsal and ventral nasal opercula resemble those of *P. psittacea* (Fig. 2).

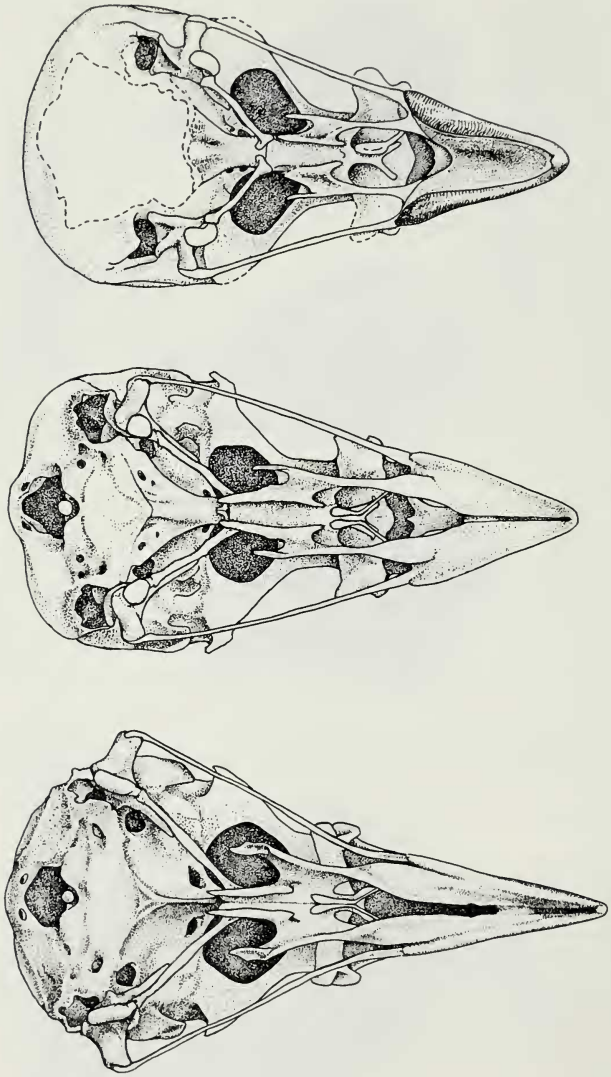

FIG. 4. Ventral view of the crania of *Dysmorodrepanis munroi* (top), *Psittirostra psittacea* (middle), and *Pseudonestor xanthophrys* (bottom).

DESCRIPTION

Size and body proportions.—The lengths of the wing chord and tail of *Dysmorodrepanis* fall 1.3 standard deviations below the mean for a series of females of *P. psittacea* (Table 1), so that if wing chord is a reliable gauge of body size, the holotype of *Dysmorodrepanis* is similar in size to

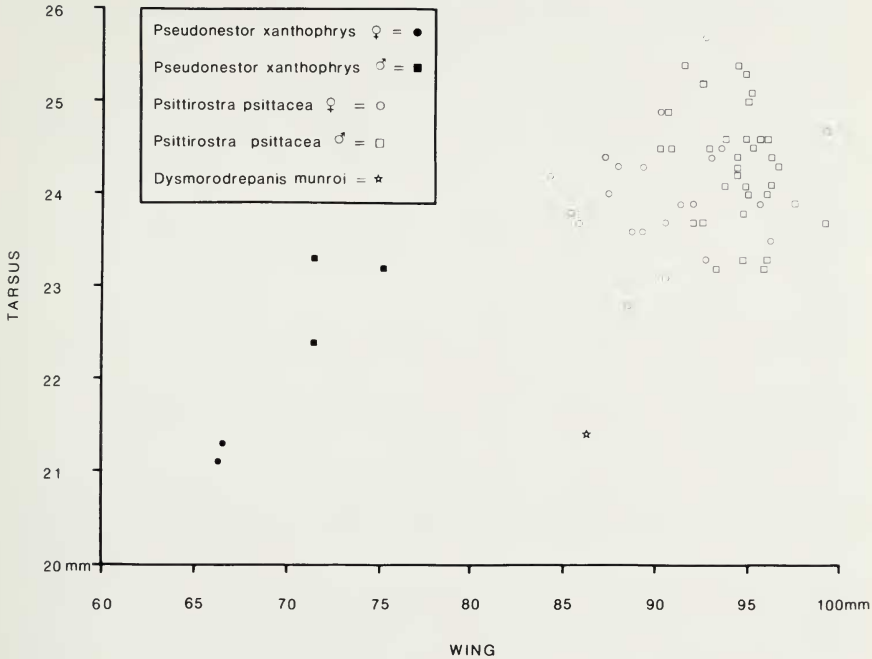

FIG. 5. Graph showing the short tarsus in relation to wing chord of *Dysmorodrepanis,* as compared to *Psittirostra psittacea* and *Pseudonestor xanthophrys.*

small females of *P. psittacea* and larger than either sex of *Pseudonestor.* Among these species, the bill is absolutely and proportionately smallest in *Dysmorodrepanis,* whose bill dimensions are three to five standard deviations below the means for females of *P. psittacea. Dysmorodrepanis* differs further from *P. psittacea* and *Pseudonestor* in that the tarsus is shorter relative to the wing chord (Fig. 5).

Plumage.—The plumage of *Dysmorodrepanis* has been adequately described by Perkins (1919) and is illustrated in the frontispiece. The specimen is rather nondescript, greenish olive above, and whitish yellow below, with a faintly indicated yellowish superciliary stripe. The most striking feature is the conspicuous wing patches formed by the broad, whitish tips and inner vanes of the secondaries. Greenway (1939:479) maintained that this was due to the specimen being partially albinistic, and he asserted that "whitish feathers are scattered indiscriminately over nape, breast and belly." In fact, there are no whitish feathers in the nape, although the feathers here have light-colored shaft streaks. The appearance of whitish feathers scattered over the ventral surface is caused by exposure of the whitish bases of the ventral feathers, but close examination shows all of these to be tipped with yellowish. The whitish patches in the secondaries

TABLE 1
SKIN MEASUREMENTS (MM) OF *DYSMORODREPANIS* AND RELATED TAXA

	Culmen length	Culmen width	Wing chord	Tarsus	Tail
Dysmorodrepanis munroi	13.0	5.0	86.3	21.4	52.0
Psittirostra psittacea, females	15.5 ± 0.8[a] (14.0–16.9)[b] 26[c]	6.6 ± 0.3 (5.7–7.0) 18	90.2 ± 3.0 (84.2–96.2) 26	23.9 ± 0.6 (22.8–25.7) 26	55.7 ± 3.1 (49.4–62.3) 28
Psittirostra psittacea, males	15.9 ± 0.7 (14.3–17.0) 35	6.6 ± 0.3 (6.0–7.1) 28	94.6 ± 2.1 (90.1–99.3) 37	24.2 ± 0.7 (22.8–25.4) 39	58.3 ± 1.7 (54.6–61.0) 35
Pseudonestor xanthophrys, females	16.4, 16.7		66.3, 66.4	21.1, 21.3	39.4, 39.9
Pseudonestor xanthophrys, males	21.1 (18.9–23.0) 6		72.8 (71.4–75.1) 6	23.0 (22.4–23.8) 6	44.4 (43.2–45.9) 5

[a] Mean ± one standard deviation.
[b] Range.
[c] Sample size.

form intricate patterns with the darker central portions of the vanes that vary from one feather to the next but are symmetrical from side to side. These appear to be perfectly normal, and neither the secondaries nor any other aspect of the plumage appears to be affected by albinism.

After examining the holotype, Amadon (1950:172) speculated that: "Perhaps because of the abnormal bill and consequent inability to feed properly, its plumage is abraded, with evidence of retarded molt." This is also untrue. Although the drab coloration and somewhat disarrayed feathers give the impression of a rather worn, faded specimen, close inspection shows that the feathers are not abraded, the remiges in particular being quite fresh. We see no evidence of abnormality of molt or coloration in the specimen of *Dysmorodrepanis munroi*. Therefore, its principal differences from females of *P. psittacea*—white patches in secondaries, superciliary stripe, lighter and more yellowish underparts—must be regarded as characteristic of the species. The completely ossified skull of the holotype shows it not to be a juvenile; it may be an adult female, as suggested by the dull plumage. If so, the male in adult plumage may have been more brightly colored, as in *P. psittacea*. Yellow underparts and a distinct superciliary stripe occur in *Pseudonestor xanthophrys*, but *Pseudonestor* has no white in the wings, and its adult plumage is brighter in both sexes than in *Dysmorodrepanis*.

External bill morphology.—*Dysmorodrepanis* resembles *P. psittacea* and *Pseudonestor* in its long, overhanging maxillary rostrum in combination with a sturdy, almost finch-like bill (Fig. 3), but it is set apart from these species by the diastema between its tomia. The maxillary rostrum of *Dysmorodrepanis* is more hooked and compressed laterally, with a more ridged culmen, than in *P. psittacea.* In this respect the bill shape is intermediate between *P. psittacea* and *Pseudonestor.* The external naris in *Dysmorodrepanis* is a slit between the dorsal and ventral nasal opercula (Fig. 2). The dorsal nasal operculum covers slightly more than half of the narial opening and has a convex ventral margin. The opercula resemble *P. psittacea* but differ from *Pseudonestor,* in which the ventral operculum is lacking and the dorsal one has a concave margin. The upturned portion of the mandibular rostrum consists of rhamphotheca: it is not supported by bone. This is also true of the tip of the maxillary rostrum in both *Dysmorodrepanis* and *P. psittacea* (Fig. 3). The rhamphotheca of *Dysmorodrepanis,* especially of the maxillary rostrum, is darker brown than most individuals of *P. psittacea,* but lighter than the maxillary rostrum in *Pseudonestor.*

Within the trough on the ventrocaudomedial surface of the maxillary rostrum, there is a plate of thickened rhamphotheca. The plate is bounded laterally by distinct ridges that turn inward at about two-thirds of the distance to the tip of the maxillary rostrum and which meet each other at the midline (Fig. 2). Similar ridges are present in *P. psittacea.*

Tongue.—Munro saved the dried tongue of *Dysmorodrepanis,* but it was subsequently lost. Perkins examined the tongue when it was already in a poor state of preservation, and commented that it agreed in general with Gadow's description of the tongue in *Loxioides* [*bailleui*] (Gadow 1891:223), adding that the tongue of *Dysmorodrepanis* "is not acute at the tip and is apparently emarginate there, with the edges microscopically serrulate" (Perkins 1919:251). From this we gather that the tongue was of the primitive drepanidine form which is nontubular, fleshy above, corneous below and caudolaterally, and has a rounded tip edged with small papillae. This tongue morphology also occurs in *P. psittacea* and other finch-like drepanidines and in some cardueline finches (Raikow 1977).

Cranial osteology.—The fully ossified cranial vault (double-plated and trabeculated) indicates that the holotype of *Dysmorodrepanis* is a mature bird. It has the thick interorbital septum and associated features that characterize the Carduelinae, including the Drepanidini (Zusi 1978). In *Dysmorodrepanis,* these features are: interorbital septum complete (not fenestrated), double-walled and supported by internal bony trabeculae throughout; ventral border of the cranial fenestra straight; the floor of the anterior cranial cavity (between the cranial fenestrae) broad and flat; and

TABLE 2

CRANIAL DIMENSIONS OF *DYSMORODREPANIS* AND *PSITTIROSTRA PSITTACEA* (MM)

	Dysmorodrepanis munroi	*Psittirostra psittacea*
Cranium length without maxilla	18.8	20.9, 21.7
Orbit length	9.9 (0.53)[a]	10.1 (0.48), 10.4 (0.49)
Ventral length of pterygoid	5.4 (0.29)	6.6 (0.31), 6.7 (0.31)
Length of jugal bar	13.3 (0.70)	16.1 (0.77), 16.1 (0.74)
Palatine length (transpalatine process to prepalatine bar)	8.1 (0.43)	11.1 (0.53)
Nostril length	3.8	5.2
Height to length ratio of nostril	0.87	0.65

[a] Numbers in parentheses are ratios of the measurements to cranium length.

the caudal edge of the septum between the optic foramina broad. The palatine process of the premaxilla is fused to the prepalatine bar in the configuration of a lateral flange. This is an apomorphous condition that characterizes drepanidines with medium to heavy bills, but it also occurs in unrelated passerines (Bock 1960).

We compared *Dysmorodrepanis* to other drepanidines with similar bill shapes (*Psittirostra psittacea,* MVZ 122619 and USNM 111454; *Pseudonestor xanthophrys,* BPBM 240 and illustrations of BM S/1961.11.40 and S/1961.11.46). The skull of *Dysmorodrepanis* is slightly shorter than in *P. psittacea,* and the orbits of these species are similar in length (Table 2).

The most striking differences between *Dysmorodrepanis* and *P. psittacea* are in the mandible (Figs. 1 and 6). The articular portion of the mandible is rotated strongly ventrad in relation to the rest of the ramus, so that the surfaces of the mandibular cotylae face caudodorsally. These surfaces face dorsad in most birds, including *P. psittacea* and *Pseudonestor.* The medial process of the mandible in *Dysmorodrepanis* is broader than in *P. psittacea* and, like the rest of the cranial articulation of the mandible, is directed more caudad compared to other drepanidines (Fig. 6).

Compared to *P. psittacea,* the mandibular symphysis of *Dysmorodrepanis* is much narrower and has the ventral surface angled strongly upward. The ramus (pars intermedia) is dramatically shorter and becomes thin and blade-like dorsally. The coronoid processes are directed more caudad than dorsad, unlike the condition in *P. psittacea* and other drepanidines. The mandibular fenestra of *Dysmorodrepanis* is smaller and more circular than in *P. psittacea.*

Dysmorodrepanis has a larger and more elongate medial condyle of the quadrate and a smaller posterior condyle than *P. psittacea,* while neither of the aforementioned species shows the extreme elongation of the medial

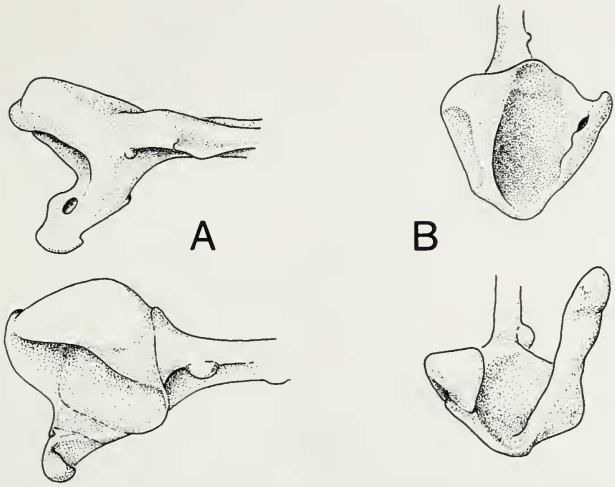

FIG. 6. Articular ends of the mandibles of *Dysmorodrepanis munroi* (above) and *Psittirostra psittacea* (below) in dorsal (A) and caudal (B) views.

condyle and reduction of the orbital process seen in the quadrate of *Pseudonestor* (Fig. 4). Compared to *P. psittacea* and *Pseudonestor,* the quadrate-squamosal articulation is placed more rostrally on the skull in *Dysmorodrepanis* (Figs. 1 and 4). Moreover, when the bill is closed the quadrate is rotated farther rostrad, as reflected by the more obtuse angle between the body of the quadrate and the jugal bar (102° in *Dysmorodrepanis,* 96° in *P. psittacea,* and 78° in *Pseudonestor*). This forward position of the quadrate leaves relatively little space for the other bones of the palate, and the palatines and jugal bar are noticeably shorter in *Dysmorodrepanis* (Table 2, Fig. 4). The maxilla of *Dysmorodrepanis* is broadly similar to that of *P. psittacea* (Figs. 1 and 3), although *Dysmorodrepanis* has a shorter and more rounded nostril opening (Table 2) and, judging from the contour of the rhamphothecal covering, a much more domed ventral surface of the maxilla (Figs. 2 and 4).

MYOLOGY

Complete descriptions of drepanidine jaw muscles are available only for several species of "*Loxops*" (Richards and Bock 1973). To salvage myological information from the unique specimen of *Dysmorodrepanis* and to look for modifications related to its peculiar bill and lower jaw, we examined the dried muscles on the skull. These were fragmentary, the entire base of the cranium having been cut away. The condition of individual muscles, which are partially illustrated in Fig. 7, is detailed below.

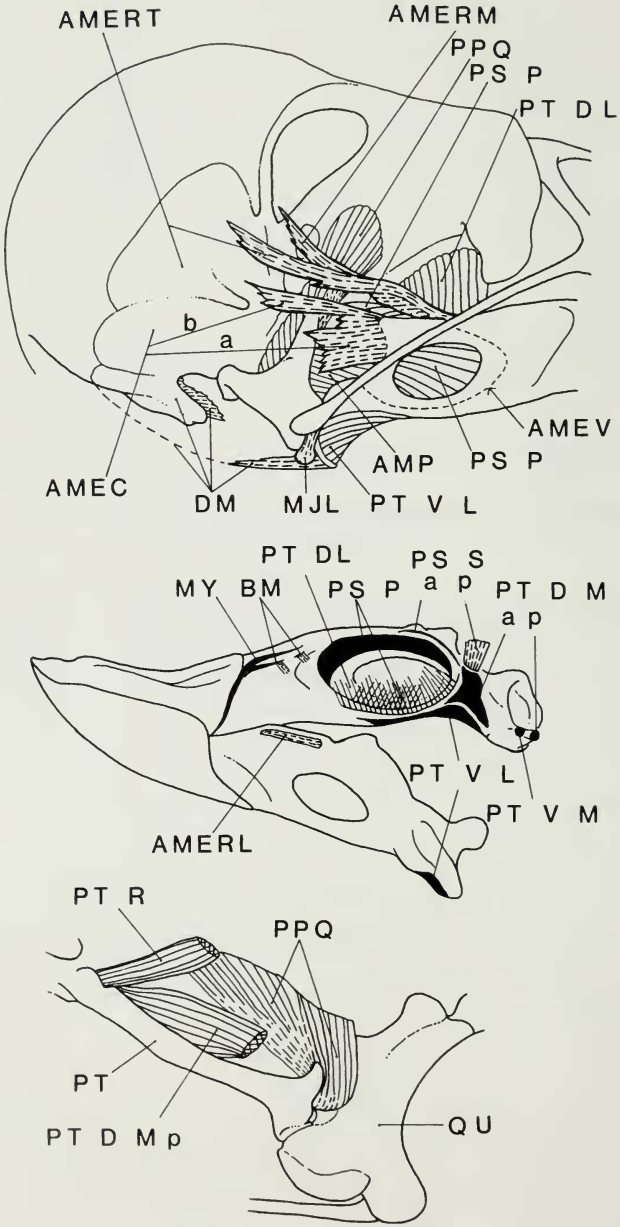

FIG. 7. Jaw muscles of *Dysmorodrepanis munroi*. Above, right lateral view of skull. Muscle fibers of adductor mandibulae, depressor mandibulae, and pseudotemporalis muscles mostly or entirely removed. Aponeuroses and tendons shaded with dashed lines. Dotted

The skull caudal to the rhamphothecae was soaked in warm water to soften the muscles, which were removed after description. Terminology for the musculature and palate follows Richards and Bock (1973).

Lateral jugomandibular and postorbital ligaments were not found. (The postorbital process had been partially removed.) The medial jugomandibular ligament is strong, attaching on the ventral surface of the jugal bar just rostral to the lateral condyle of the quadrate. It wraps around the articulation to attach in a notch on the caudal edge of the articular, just lateral to the occipitomandibular ligament. A sesamoid is enclosed at a bend of the ligament caudomedial to the lateral cotyla of the mandible; the ligament and sesamoid anchor the caudodorsal and caudoventral portions of the articulation capsule.

M. depressor mandibulae.—The superficial portion (b [and c?], Richards and Bock 1973) had been removed except for part of the aponeurosis of insertion attaching along the caudoventral edge of the articular. A scar along the lateral surface of the tympanic wing of the exoccipital and adjacent surface of the cranium is similar to, but less well defined than that of *Psittirostra.* The deeper portion (a of Richards and Bock 1973) originates from an aponeurosis along the craniolateral rim of the tympanic wing of the exoccipital. It inserts by a sheet-like aponeurosis, attaching adjacent and deep (caudal) to that of the superficial portion on the rim of the articular. Attachment continues medially along the ventral border of the articular, superficial to the medial jugomandibular ligament and its sesamoid, to its limit on a knob of the medial process of the mandible caudal to the osteum tubae. Here, aponeuroses of origin and insertion meet and thicken into a ligament (occipitomandibular) from the ventral edge of the exoccipital.

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line on mandible is limit of adductor mandibulae externus ventralis. Middle, left dorsolateral view of mandible. Tendons shaded with dashed lines, aponeuroses represented by parallel lines, fleshy attachments shown in black. Semidiagrammatic. Below, medial view of right quadrate and pterygoid. Abbreviations: A M E C a, b, M. adductor mandibulae externus caudalis (parts a, b); A M E R L, M. adductor mandibulae externus rostralis lateralis; A M E R M, M. adductor mandibulae externus rostralis medialis; A M E R T, M. adductor mandibulae externus rostralis temporalis; A M E V, M. adductor mandibulae externus ventralis; A M P, M. adductor mandibulae posterior; BM, M. branchiomandibularis; D M, M. depressor mandibulae; M J L, medial jugomandibular ligament; MY, M. mylohyoideus (=M. intermandibularis); P P Q, M. protractor pterygoidei et quadrati; PS P, M. pseudotemporalis profundus; PS S a, p, M. pseudotemporalis superficialis (anterior, posterior parts); PT, pterygoid; PT D L, M. pterygoideus dorsalis lateralis; PT D M a, p, M. pterygoideus dorsalis medialis (anterior, posterior parts); PT R, M. pterygoideus retractor; PT V L, M. pterygoideus ventralis lateralis; PT V M, M. pterygoideus ventralis medialis; QU, quadrate.

The depressor mandibulae is relatively large in the species studied by Richards and Bock (1973), occupying a major part of the lateral portion of the cranium and inserting, in part, on a long retroarticular process. To judge from muscle scars, the muscle in *Dysmorodrepanis* had a more restricted attachment on the cranium, and the retroarticular process is entirely lacking. The superficial part probably covered most or all of the deep part. The insertion is entirely aponeurotic, perhaps because the unusual orientation of the articular surfaces leaves only a narrow rim of the articular for attachment.

M. adductor mandibulae externus.—This muscle complex had been removed, except for some fibers of ventralis on the lateral surface of the ramus, and parts of the aponeuroses of insertion of rostralis medialis, rostralis lateralis, rostralis temporalis, and caudalis, on the mandible. The aponeuroses of insertion of rostralis temporalis and medialis converge from either side of the postorbital process to make a single, strong attachment on the anterior coronoid process. This "process" consists of a raised scar that begins on the dorsolateral surface of the ramus and extends caudally and somewhat medially along the dorsal rim of the ramus, almost to the posterior coronoid process.

Aponeuroses of insertion of caudalis are confluent but distinguishable; that of part b is longer and stouter, attaching on the caudodorsal surface of the posterior coronoid process. That of part a is continuous ventrally with aponeurosis a, forming a vertical sheet shorter and thinner than the latter; it attaches on a vertical crest of the lateral surface of the ramus continuous with the caudal face of the posterior coronoid process.

The attachment of ventralis is not marked on bone except for its caudoventral border along the ventrolateral ridge of the ramus. Scattered muscle fibers indicate that it occupied the lateral surface of the ramus, immediately rostral and ventral to the mandibular fenestra, and much of the mandibular surface caudal and caudodorsal to the fenestra.

Rostralis lateralis inserts by a slender aponeurosis that parallels the dorsolateral edge of the ramus and attaches rostral to the mandibular fenestra.

M. adductor mandibulae posterior.—The muscle had been removed, except for a thin sheet of fibers from the ventral edge of the base of the orbital process of the quadrate. The fibers attach on the dorsal and dorsolateral surfaces of the ramus, between the lateral protuberance of the ramus (just rostral to the lateral cotyla) and the pseudotemporal tubercle.

M. pseudotemporalis superficialis.—The muscle had been removed, except for parts of the tendons of insertion and some fibers of origin attached to depressions on the rostral wall of the cranium and on aponeuroses

from two intraorbital crests. This muscle has both anterior and posterior portions. Attachment of the posterior portion is by a complex of strong aponeuroses to the pseudotemporal tubercle of the mandible. The anterior portion inserts by a thin, sheet-like aponeurosis and some fleshy fibers along the dorsomedial surface of the ramus between M. pseudotemporalis profundus and the coronoid processes. Its linear attachment extends from the pseudotemporal tubercle to the rostral limit of the anterior coronoid process.

M. pseudotemporalis profundus.—A large muscle arising fleshy from the ventrolateral and ventromedial surfaces of the distal two-thirds of the orbital process of the quadrate and by strong aponeurotic sheets from the tip, ventral edge, and medial surface of at least the distal half of the process. The aponeurosis from the tip of the orbital process lies along the rostral surface of the muscle. Fibers attach on the medial surface of the mandible around the mandibular fenestra, with strongest attachment by an aponeurotic sheet on the thickened, ventral portion of the ramus.

M. pterygoideus.—Much of the muscle mass had been cut away ventromedially and in the orbit; the left pterygoid bone had been cut and the mediopalatine processes removed. All descriptions are incomplete.

Dorsalis lateralis has an extensive attachment on the lateral surface of the palatine blade, base of the prepalatine bar, and dorsolateral surface of the transpalatine process and its aponeuroses. Its mandibular attachment is by an aponeurotic sheet along a narrow line ventral to the ventral attachment of M. pseudotemporalis profundus, and between points slightly rostral and caudal to the mandibular fenestra.

Ventralis lateralis attaches by aponeuroses to the transpalatine process and palatine blade. The mandibular attachment is fleshy on the caudoventral, caudomedial, and caudolateral portions of the ramus and on the base of the medial process. Species studied by Richards and Bock (1973) showed little or no attachment on the lateral surface of the mandible.

Ventralis medialis extends from the tip of the transpalatine process to the tip of the medial process of the mandible. Both attachments are aponeurotic.

The anterior part of dorsalis medialis extends from the palatine hasp and pterygoid to the medial surface of the mandibular ramus, bounded by insertions of pterygoideus dorsalis lateralis, pseudotemporalis superficialis (posterior portion), pterygoideus ventralis lateralis, and by the jaw articulation. The posterior part extends from the dorsocaudal portion of the pterygoid bone to the tip of the medial process of the mandible (caudalmost angle of the blunt-tipped medial process).

The retractor portion originates on the ventral surface of the braincase

rostral to the basitemporal plate. It inserts on the rostrodorsal portion of the pterygoid and on the retractor process of the pterygoid and dorsal surface of the prepalatine process.

M. protractor pterygoidei et quadrati.—Origin of the pterygoidei portion is from a marked depression on the wall of the interorbital septum, between the cranial fenestrae and palatine hasp. It extends rostrad halfway between the rostral limits of the cranial fenestra and optic foramen (on an imaginary transverse plane perpendicular to the jugal bars). Insertion is by a short tendon on the dorsal process of the pterygoid. Origin of the quadrati portion on the skull had been removed. Its insertion is marked by a depression on the medial surface of the body of the quadrate extending to the dorsal edge of the base of the orbital process. Fibers of the two parts of this muscle merge.

M. branchiomandibularis.—Most of this muscle had been removed. Part (?) of its mandibular attachment remained. The origin is partly fleshy and partly tendinous along a narrow line on the dorsomedial surface of the ramus, lying ventral to the attachment of M. mylohyoideus and extending from the caudal limit of the rhamphotheca halfway to the rostral limit of the mandibular fenestra.

M. mylohyoideus (=M. intermandibularis).—The muscle had been removed except for part (?) of its mandibular attachment. It originates fleshy along a narrow line on the dorsomedial surface of the mandibular ramus just dorsal to M. branchiomandibularis. Its origin extends rostromedially almost to the midline of the mandibular symphysis just ventral to the rhamphotheca. The caudal limit of origin appears to be close to that of M. branchiomandibularis.

Scars of neck muscles on the occiput (*M. complexus, M. biventer cervicis,* M. splenius capitis), are comparable in strength and position to those of *Psittirostra psittacea.*

To judge from the incomplete material examined, *Dysmorodrepanis* shows no major departure from the general pattern of jaw musculature of the drepanidines studied by Richards and Bock (1973), although the adductor muscles of the mandible are relatively larger and the depressor of the mandible relatively smaller. The adductor muscles of *Dysmorodrepanis* appear to be somewhat less strongly developed than in *Psittirostra psittacea,* but the protractor of the upper jaw was probably at least as well developed (based on muscle remains, on the limits and depth of muscle scars, and on the prominence of crests and processes). The mandibular depressor is, perhaps, less strong than that of *Psittirostra psittacea.* In contrast to *Pseudonestor xanthophrys,* the retractor portion of M. pterygoideus is not enlarged (Zusi 1989).

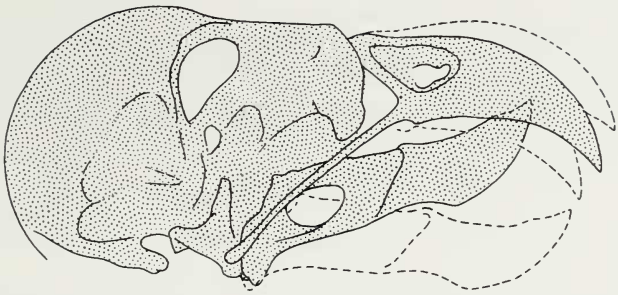

FIG. 8. The skull of *Dysmorodrepanis munroi* showing hypothetical kinetic movements of the jaws.

FUNCTIONAL ANATOMY

After soaking the skull of *Dysmorodrepanis,* we were able to move the upper jaw well above and below the closed position. We made no attempt to measure this movement, but the positions illustrated in Fig. 8 are probably representative of movements in the living bird. In the closed bill, about 40% of the tomial length of the maxillary rostrum extends beyond the lower mandible, but in the opened bill the tips of the rostra oppose each other like ice tongs (Fig. 8). The tips can be made to meet when both jaws are depressed beyond the resting position.

The blunt surfaces of the tomial crests, which extend over the caudal two-thirds of the diastema on both jaws, lie opposite each other with the bill in closed position. If either jaw moves independently, or if both are depressed beyond the closed position, the blunt surfaces are no longer opposite. They remain more or less opposite if both jaws open or close simultaneously. Neither the tips nor the tomia showed irregularities or noticeable wear, and the flattened surfaces were not abraded.

It is unlikely that the bird crossed its bill tips in the manner of crossbills (*Loxia*) even occasionally. The tips are not asymmetrical or worn in the area of potential crossing, they are not laterally compressed, and the jaw articulations are not asymmetrical. Certain features of the jaw articulation imply that lateral rotation of the mandibular rostrum was extremely limited as discussed below. The diastema was thus a permanent feature of the closed bill.

The mandible of *Dysmorodrepanis* slopes ventrally relative to the long axis of the jugal bar, both rostral and caudal to the mandibular fenestra (Fig. 8). The rostral slope relates to the "open-mouthed" position of the closed jaw required by the recurved rhamphotheca. The caudal slope has several consequences. One is that the surfaces of the mandibular cotylae

lie at an angle of about 60° to the long axis of the lower jaw (from the articulation to the tip) in lateral view. The comparable angle in *Psittirostra psittacea* is 13°. In the latter species, lateral motion of the lower jaw requires unilateral sliding of the articular on the quadrate; this sliding is possible because the planes of motion of the jaw and articular surface are approximately coincident. In *Dysmorodrepanis* the planes are widely divergent; lateral motion of the jaw would lift the articular of the opposite side off the quadrate. Unilateral sliding of the jaw on the quadrate would produce rotation of the lower jaw about its median axis.

Configuration of the condyles of the quadrate and cotylae of the lower jaw further suggests that sliding occurs in *P. psittacea* but not in *Dysmorodrepanis.* The profile of the medial cotyla in longitudinal section is convex upward in the former—concave upward in the latter. The larger medial condyle of the quadrate of *Dysmorodrepanis* occupies most of the medial cotyla in a loose ball-and-socket arrangement. Reduced capacity for sliding is further reflected by the short lateral cotyla. Manipulation of the lower jaw on the skull confirms that the articulation acts essentially like a pin hinge. This would ensure that the mandibular rostrum closed into the groove of the maxillary rostrum without damaging the tomia.

DISCUSSION

Several facts suggest that the bill of *Dysmorodrepanis* was not used often for strong biting or crushing or forceful manipulation of the substrate: the adductor musculature is not highly developed, the flattened portions of the tomia of the lower jaw are not supported by bone, and the domed lingual contours of the rostra provide poor surfaces for biting. The shape of the rostra and the presence of a diastema appear unsuited for insect gleaning or handling of small seeds. Munro (1944) noted that when he collected *Dysmorodrepanis* the stomach and throat were full of the small ripe berries of *Urera glabra,* a widely distributed native Hawaiian shrub. *Dysmorodrepanis* may have used the pincer action of its bill tips to pluck berries or flowers, and the blunt tomial surfaces of the diastema could have functioned to carry or to crush fruit such as medium-sized berries. On the other hand, the berries in the stomach of *Dysmorodrepanis* could represent an opportunistic meal rather than the mainstay of its existence. A diet of berries is an unlikely source for the selection that produced the unusual bill of *Dysmorodrepanis,* considering that a great many avian species feed on berries and none of them has developed a similar adaptation.

Another possibility, albeit a highly speculative one, is that *Dysmorodrepanis* was a specialized snail-eater. Native land snails were once an abundant source of potential nourishment in the Hawaiian islands before

human habitat disruptions drastically reduced their numbers and distribution. These were both arboreal and terrestrial and ranged in adult size from a few millimeters up to several centimeters in length. Other Hawaiian passerines may take small snails on occasion, but the only species known to feed on them frequently is *Melamprosops phaeosoma* on Maui (Baldwin and Casey 1983), a drepanidine with an ordinary but rather weak finch-like bill. *Dysmorodrepanis* could have used the pincer action of its bill or the diastemal tomia to transport snails. The hooked maxillary rostrum may have been capable of spearing the body and drawing it out of the shells of larger snails as Snail Kites (*Rostrhamus sociabilis*) do. The incurled tomial crests of the diastema could have crushed the shells of medium-sized snails, and the fleshy tongue might then have maneuvered the broken shells out the open sides of the bill, and the meat into the throat.

There is no reason to assume that the natural distribution of *Dysmorodrepanis* was limited to the island of Lanai. Fossil evidence has shown that the distribution of many endemic Hawaiian birds was wider in the past. *Dysmorodrepanis* is most likely to be found as a fossil on Maui or Molokai, two adjacent islands that were connected to Lanai as recently as 17,000 years ago. No fossils of *Dysmorodrepanis* have been identified to date, however (Olson and James 1982, 1984; James 1987; James et al. 1987).

Despite the general reluctance among ornithologists to give due consideration to taxa that are known from unique specimens, the case of *Dysmorodrepanis* is not at all singular or unexpected. Over the past century, the decline of native birds on Lanai has been so dramatic that seven of the eight endemic Hawaiian species known from non-fossil specimens are now apparently extinct there (Scott et al. 1986). Only three specimens of the Lanai Akialoa (*Hemignathus lanaiensis*) were procured before that species became extinct. Elsewhere in the Hawaiian islands, *Myadestes oahuensis* and *Hemignathus lichtensteini* are each known from two specimens, *Chaetoptila angustipluma* is known from four, *Ciridops anna* is known from five, and *Porzana sandwichensis* is known from seven. Similar cases from the southwest Pacific are *Aplonis mavornata* from the Cook Islands (Olson 1986) and *Aegotheles savesi* from New Caledonia (Olson et al., in press), each known from a single specimen. What these rare specimens reflect is the acceleration in avian extinctions that accompanied human proliferation in the Pacific basin.

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COLOR PLATE

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